

Primary Divergence and Species Concepts in Ferns

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Primary divergence may be defined as differentiation among populations of homoploid organisms caused by natural selection; it often results in the formation of new species or subspecies. This definition excludes the relatively instantaneous processes of polyploidy and hybrid species formation. Monographers of pteridophyte genera name and describe species and have perforce been the individuals forced to deal with problems of primary divergence and the delimitation of species. Since scant literature exists addressing species concepts for pteridophytes, we have contrasted specific examples of usage from modern systematic treatments by various workers.

We examined a sample of 50 monographs completed during the last 50 years by 36 authors (Table 1). Only 12 (24%) of these monographs contained any explicit discussion of the criteria for the species concepts and/or infraspecific categories employed, so that our analysis of these topics is based largely on inference. We perceive that three general types of species concepts have been used singly or in concert by pteridologists: the biological, morphological, and (for lack of a better term) "look-alike" concepts.

The biological concept is used here in the somewhat restricted sense of genetic intersterility between species and states that if two taxa can cross to produce fertile offspring, then they are the same species. This concept has rarely been used in fern systematics because data on cross-fertilization is difficult to obtain. Hennipman and Roos (1982), however, used the ability of gametophytes to cross as evidence for reducing four taxa accepted by Hoshizaki (1972) as species to subspecies or varieties of *Platycerium bifurcatum*, even though the subsumed taxa were geographically and/or ecologically distinct.

In contrast, the morphological concept is the recognition of discrete taxa on the basis of breaks of form, with no knowledge of the ability to hybridize. Of course, what constitutes such morphological discontinuities can be quite subjective and contentious. This concept is the tacit species concept of most fern monographers who have worked from herbarium specimens alone.

The look-alike concept is similar to the morphological concept (and might best be considered a subset of it) in that both delimit taxa by morphological discontinuities. It differs, however, in that it classifies taxa hierarchically as species or varieties based upon relative morphological similarities—an author may classify two morphologically distinct entities as varieties because they "look alike," when by strict morphological criteria they might otherwise have been treated as separate species. An example is the *Lycopodium obscurum* complex studied by Hickey (1977). He clarified the taxonomy of this group by showing that a new taxon, *L. isophyllum*, was morphologically distinct from *L. obscurum* and *L. dendroideum*. Hickey classified *isophyllum* as a variety of *L. obscurum* rather than as a separate species, because of closer resemblance of

these two taxa than either to *L. dendroideum*. Thus the use of the varietal designation was intended to imply phylogenetic affinity of two distinct taxa (Hickey, pers. comm.). Johnson (1986) also used this concept in recognizing two distinct, nonintergrading taxa as subspecies of *Marsilea vestita*.

SUBSPECIES AND VARIETIES

Infraspecific categories must be considered in relation to species concepts when discussing primary divergence, because one person's species is often another person's subspecies or variety. Infraspecific categories are frequently used by monographers; of the 50 monographs surveyed (Table 1), 33 (66%) included subspecies, varieties, or both. As with species concepts, the definitions of infraspecific categories were rarely discussed and had to be inferred from the author's work. In some instances it was impossible to determine why a monographer used an infraspecific instead of specific category.

Subspecies were used in 11 (22%) of the monographs that we surveyed (Table 1) and were more consistently defined than varieties. Subspecies were generally used to describe geographic variation that either varied continuously (i.e., without sharp morphological breaks; e.g., Clausen, 1938, in *Botrychium multifidum*) or varied discontinuously and was based on a single character (e.g., Johnson, 1986, in *Marsilea vestita*). Subspecies have, however, also been used to name cytotypes (Gastony & Windham, this symposium).

Varieties were used in 29 (58%) of the monographs surveyed (Table 1). There was a general lack of consistency in how varieties were defined and a few monographs contained examples of more than one kind of variety within a single genus. All of the definitions used for subspecies were also used for varieties by various monographers. Where nonintergrading geographic variation was recognized, either a single character (e.g., Stolze, 1981, in *Cnemidaria uleana*) or several "insignificant" characters were cited, usually involving indument density, slight differences in leaf-cutting, or microscopic features (e.g., Gastony, 1973, in *Nephelea woodwardioides*). In some cases, monographers chose to describe the minute, nonintergrading character variation without resorting to formal taxonomic designation (e.g., Moran, 1986, in *Olfersia cervina*).

Varieties were also used to describe nongeographic variation (e.g., Stolze, 1981, in *Cnemidaria mutica*). Autopolyploids, allopolyploids, and hybrids have also been named as varieties (Barrington et al., this symposium; Gastony & Windham, this symposium). Finally, as noted above, in some cases varieties were simply named without any discussion, and we were unable to infer from the publication on which kind of character(s) the taxon was based.

The inconstancy of usage of the varietal and subspecific categories has long been a problem in systematics. Because there has been little attempt to standardize the definitions for these terms, particularly when applied to taxa involving primary divergence, it would seem that this problem will remain with us in the future. Although the *International Code of Botanical Nomenclature* recognizes variety as the primary level of infraspecific classification, we prefer the term subspecies for situations involving geographically defined variation,

TABLE 1. Data Compiled from 50 Recent (1938–1987) Monographs of Fern Genera. Monographs that discuss species concepts = 12 (24%). Monographs using infraspecific categories = 33 (66%); subspecies = 11 (22%); varieties = 29 (58%); molecular data = 3 (6%); cladistics = 16 (32%).

Author	Taxon	Spp.	Infraspecific categories used		Discussion of sp. concept	Studies	
			subsp.	var.		molecular	cladistic
Alston et al. 1981	Selaginella	133	+	+	-	-	-
Barrington, 1978	Trichipteris	55	-	+	-	-	-
Bishop, 1978	Cochlidium	16	-	-	-	-	-
Blasdell, 1963	Cystopteris	10	-	+	-	-	+
Boer, 1962	Didymoglossum & Microglossum	19	+	-	-	-	-
Brown, 1964	Woodsia	22	-	+	-	-	+
Clausen, 1938	Botrychium & Ophioglossum	50	+	+	+	-	-
Conant, 1983	Alsophila	30	+	-	-	-	-
de la Sota, 1966	Polypodium squamatum group	22	-	-	-	-	-
Evans, 1969	Polypodium pectinatum- plumula	26	-	+	-	-	+
Gastony, 1973	Nephelea	18	-	+	+	-	-
Haufler, 1979	Bommeria	4	-	-	-	+	+
Hauke, 1963	Equisetum subg. Hippochaete	7	+	+	-	-	+
Hennipman, 1977	Bolbitis	41	+	+	-	-	-
Hennipman & Roos, 1982	Platycterium	15	+	+	+	-	+
Holttum, 1971	Stenochlaena	6	-	-	-	-	-
Holttum, 1975	Syngamma	17	-	-	-	-	-
Holttum, 1986	Triplophyllum	20	-	-	+	-	-
Hovenkamp, 1986	Pyrrosia	51	-	+	-	-	+
Johnson, 1986	Marsilea	12	+	-	-	-	-

Kramer, 1957	Lindsaea	45	+	+	+	-	-
Lellinger, 1971	Plagiogyria	6	-	-	-	-	-
Lellinger, 1972	Niphidium	10	-	-	-	-	+
Lellinger, 1984	Hymenophyllopsis	8	-	-	-	-	-
Lloyd, 1971	Onocleoids	5	-	-	-	+	-
Mickel, 1962	Anemia subg. Coptophyllum	38	-	+	-	-	+
Moran, 1986	Olfersia	1	-	-	-	-	+
Moran, 1987	Polybotrya	35	-	-	-	-	+
Parris, 1983	Grammitis	64	-	-	-	-	-
Ravensburg & Hennipman, 1986	Pyrrosia	6	-	+	-	-	+
Riba, 1967	Alsophila	13	-	+	-	-	-
Roos, 1985	Drynaria	31	-	-	-	-	+
Smith, 1971	Thelypteris subg. Cyclosorus	17	-	+	-	-	-
Smith, 1980	Thelypteris subg. Steiropteris	22	-	+	-	-	-
Smith, 1986	Cyclodium	10	-	+	+	-	-
Stolze, 1974	Cnemidaria	23	-	+	-	-	-
Tindale, 1965	Lastreopsis	33	+	-	-	-	-
A. Tryon, 1957	Pellaea	15	-	+	-	-	-
A. Tryon, 1970	Eriosorus	25	-	+	-	-	-
R. Tryon, 1941	Pteridium	1	+	+	-	-	-
R. Tryon, 1942	Doryopteris	26	-	+	+	-	-
R. Tryon, 1955	Selaginella rupestris group	38	-	+	+	-	-
R. Tryon, 1956	Notholaena	58	-	+	-	-	-
R. Tryon, 1960	Dennstaedtia	11	-	-	+	-	-
R. Tryon, 1962	Pityrogramma	14	-	+	+	-	-
R. Tryon, 1976	Cyathea	40	-	+	+	-	-
Wagner, 1952	Diellia	5	-	-	-	-	+
Wilce, 1965	Lycopodium sect. Complanatum	15	-	+	+	-	+
Windisch, 1978	Sphaeropteris	6	-	-	-	-	-
Yatskievych, 1989	Phanerophlebia	8	-	+	-	+	+

because it has historically been restricted to this usage, and because variety has been used so many different ways that it is *a priori* impossible to discern what the term refers to. Such usage of the term subspecies would also agree with its use by zoologists. In any event, monographers using the varietal designation in future studies would be well advised to state their criteria for the use of this level.

MODERN TRENDS AND HOW THEY AFFECT SPECIES CONCEPTS

Several trends have become apparent in how pteridologists study variation. These include more field work (and an increasing emphasis on populational studies), cladistic and/or phenetic analysis of data, and the incorporation of biochemical and molecular sources of evidence into taxonomic studies.

Field work.—One trend is the increase of field work by monographers. This is particularly true for studies involving ferns with large fronds, thick rhizomes, or other structures poorly preserved on herbarium specimens. Field studies allow collection of data not available from herbarium specimens alone, such as information on habitat, ecology, phenology, and species interactions. In addition, field work provides the opportunity to collect anatomical and cytological material, the study of which gives evidence for the delimitation of species. Field work can be especially helpful when related species grow in the same habitats, forming a “genus community” (Wagner & Wagner, 1983).

Field research is often correlated with another important trend—the analysis of inter- and intrapopulational variation. Examination of such variation has proven important in assessing the degree to which morphological characters actually serve to distinguish taxa. An example comes from Moran (1987b), who found during field work on *Polybotrya* (a genus with strongly dimorphic sterile and fertile fronds) that three morphotypes with lobed pinnae, which traditionally had been treated as separate species, actually represented unusual individuals bearing intermediate sterile-fertile leaves and belonged to a single species.

Data from interpopulational studies also have been used to document and describe geographic clines for morphological characters (Tryon, 1971, 1986; Moran, 1987a). Most of the experimental approaches to the study of plant evolution require examination of intra- and interpopulational variation before these approaches can be applied to questions at the species level (discussed below).

Cladistic and phenetic analyses.—Some pteridologists have attempted to quantify their findings, especially if they have generated large amounts of data. Quantification normally takes one of two forms: phylogenetic (= cladistic) analyses, or various phenetic analyses involving multivariate measures of similarity or dissimilarity (e.g., principal components, clustering). An explanation of these methods is beyond the scope of this paper, but interested readers are referred to the brief, but excellent general introduction by Simpson (1986). Although phenetic and cladistic analyses have not been widely used by

fern systematists (Table 1), the recent emphasis on experimental data sources will undoubtedly increase the use of quantitative methods of analysis, if only so that investigators can more efficiently deal with the often voluminous data they generate.

Underlying cladistic precepts such as paraphyly (the origin of a segregate taxon from within a derived portion of an ancestral group) greatly constrain the kinds of taxonomic assignments cladists can make. Examples of numerical cladistic analyses include those of Hennipman and Roos (1982) on *Platyserium*, Roos (1985) on *Drynarioideae*, Hovenkamp (1986) on *Pyrrosia*, and Moran (1987a) on *Polybotrya*. Several other studies have employed cladistic methods in formalizing classifications or interpreting evolutionary trends without resorting to numerical cladistic analyses. Examples of nonstatistical cladistic studies include those of Hickey (1986) on *Isoetes* and Moran (1986) on *Olfersia* and *Polybotrya*. Cladistic analysis of morphological data is complicated by the difficulties of coding and polarizing complex characters and high levels of homoplasy. Cladistics, however, can have great utility in developing evolutionary hypotheses from more conservative types of information, such as restriction site mutational analysis of chloroplast DNA (e.g., Yatskievych et al., 1988, on polystichoid ferns).

A recent example of phenetic analysis is that of Waterway (1986) on two species of *Lycopodium*. Using statistical methods, Waterway found that the correlation among a suite of characters supported the separation of *L. lucidulum* and *L. porophilum*, which had previously been considered conspecific by some authors. In addition to primarily morphometric studies, multivariate analyses have also been performed on several types of experimental data, notably in flavonoid and isozyme studies.

The advantages of statistical analysis include reproducibility of results and effective condensation of potentially overwhelming amounts of information. Quantitative approaches to taxonomic study also have implications for how researchers view species limits, since taxonomic assignments resulting from such studies are based on various statistical levels of significance. Because quantitative measures theoretically compare all taxa in a study group against the same "yardstick," relative affinities are more easily assessed than by qualitative methods.

Biochemical and molecular approaches.—Most of the biochemical and molecular research on pteridophytes has focused on speciation involving hybridization and/or polyploidy, and its use for studies on primary divergence and species delimitations remains to be adequately addressed. Of the various techniques currently in use, three sources of data show the greatest promise for elucidation of primary series limits: secondary compounds, isozymes, and nucleic acids.

Secondary compounds, particularly flavonoids, have been a staple of experimental systematics during the last 25 years. A recent use of flavonoid analysis in a problem involving primary divergence is the work of Seigler and Wollenweber (1983). They showed that, in the absence of clear morphological characters, the diploid *Notholaena standleyi* was statistically separable into

three groups of populations on the basis of geography, substrate preferences, and types of flavonoid exudates. Although the flavonoid evidence suggests that these taxa probably do not interbreed, they have not been formally named. Thus, in this case, the data from experimental sources have not (yet) affected species recognition.

Several comparative analyses of enzyme variation have proven the usefulness of measuring both intra- and interpopulational variation (see most other papers, this symposium). Although much of the recent work involving pteridophytes has focused on polyploid or hybrid speciation, a recent study by Werth et al. (1985) on the Appalachian *Asplenium* complex had bearing on the question of primary divergence. They showed that *A. rhizophyllum*, one of the three diploid species in the complex (often segregated as *Camptosorus*) was more closely related genotypically to *A. platyneuron* than was *A. montanum*, a "typical" *Asplenium*. Other recent isozyme studies also include data on primary divergence: Haufler (1985) upheld the distinctions between three morphologically defined species of *Bommeria*, but combined two other taxa under *B. subpaleacea*, and Yatskievych (1989) upheld the distinctions between two morphologically similar species of *Phanerophlebia*.

Few studies have been published on ferns involving comparative analysis of nucleic acids; however, many of the molecular techniques now available provide highly conserved characters for analysis of primary divergence. Stein et al. (1979) used evidence from DNA denaturation/renaturation studies to challenge an existing hypothesis, based primarily on paleobotanical evidence, concerning species relationships in North American *Osmunda*. More recently, Stein et al. (1986) presented qualitative comparisons of the chloroplast genomes of these species in support of the earlier molecular data. These studies did not, however, affect the status of the species previously recognized in *Osmunda*.

Yatskievych et al. (1988) presented a cladistic study of restriction site mutations in the chloroplast genomes of groups of morphologically similar species of *Polystichum* and *Phanerophlebia*. They showed that the presence of vein-anastomoses, which was previously thought to be of major importance for classification within *Phanerophlebia*, arose twice, and that free-veined *P. nobilis* and net-veined *P. remotispora* were conspecific. They also found that *Polystichum munitum* and *P. imbricans*, both from the Pacific Coast of North America, are quite dissimilar based on their chloroplast DNAs even though they are morphologically (Wagner, 1979) and isozymically (Soltis & Soltis, 1987) very similar. These data are in agreement with those of Soltis and Soltis (1987) on the chloroplast genomes of various populations of this species pair.

In most molecular studies the underlying genetic basis of the taxonomic characters is readily verifiable. Molecular researchers generally examine genotypic, rather than phenotypic, variation, data that can provide strong, indirect evidence of crossability between taxa. The species accepted thus come closer to biological rather than morphological species, even though no direct evidence of crossability has been examined. In this way, molecular studies allow pteridologists to test whether species previously defined by the morphological concept are also valid species by the biological concept.

SUMMARY

Although monographers of fern genera rarely discuss criteria for their specific and infraspecific categories, three types of species concepts have been used by pteridologists: the biological, morphological, and look-alike concepts. Infraspecific categories were used by 66% of the monographs surveyed, and in some instances it was impossible to determine why a monographer used an infraspecific instead of the specific category. The term "variety" has lost meaning since it is defined in so many ways that it is impossible to know *a priori* what kind of variation it was intended to denote. Monographers are urged to define this term explicitly when using it in future publications.

In ferns, newer data sources have not been widely used to study primary divergence and have had varying effects on species recognition. The increase of field studies has sharpened species recognition by allowing the collection of data unavailable from herbarium specimens alone. Field work also allows the study of inter- and intrapopulational variation, the lack of which has often resulted in the same species being described more than once. The increase of cladistic studies has had limited effect on species recognition in ferns, because species limits have largely been predefined before these studies were done. Quantitative methods have rarely been used in fern taxonomy and no new species have been named based on such methods. The increase of biochemical and molecular approaches has in most cases supported morphological species; however, two examples were found where species were combined on the basis of such evidence.

Molecular and biochemical data sources have been used primarily to address relative degrees of interspecific relationships (i.e., in refining classifications), rather than to recognize species. This may partially be explained by the fact that practical taxonomists have avoided naming "cryptic" species, i.e., those entities not readily separable by macromorphological characters (Paris et al., this symposium), because experimental evidence is generally not useful in distinguishing taxa in the field or herbarium. Molecular studies, which can detect lack of gene flow, may prove useful in allowing pteridologists to test whether morphological species are also species in the biological sense.

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